

Seed dispersal of *Hibbertia hypericoides* (Dilleniaceae) by ants

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Abstract

The "Yellow Buttercup", *Hibbertia hypericoides* occurs abundantly in association with several different vegetational types in the south west of Western Australia. In remnant urban bushland at Perth, Western Australia, seeds are collected by two *Mclophorus* species, *Rhytidoponera violacea* (Forel) and *Iridomyrmex discors* (Forel). In banksia low woodland at Cooljarloo, a species of the *Iridomyrmex rufoniger* group and *Rhytidoponera violacea* (Forel) collect seeds of *H. hypericoides*. One of the *Melophorus* species discriminates between potentially viable seeds, which are enclosed by a pulpy aril and non-viable seeds which show only a thin, short aril. Large numbers of potentially viable seeds are collected; the aril is consumed and the seeds discarded in the refuse heaps of the colony. The aril is rich in lipids, and the most common fatty acid in both seed and aril is oleic acid. Preliminary laboratory experiments indicate that seed germination is similar in sand collected around ant nests and sand collected elsewhere in the same habitat.

INTRODUCTION

Many Australian native plants produce seeds with fleshy and highly nutritious appendages, called food bodies or elaiosomes (Sernander 1906; Berg 1975). In numerous plants these are the arils, structures growing from some part of the ovule, or funicle, after fertilization (Corner 1976; Takhtajan 1991). Ants, attracted to the elaiosome, may carry the whole diaspore (seed plus elaiosome) to their nest and consume the food body but leave the seed intact. Such seed dispersal is called myrmecochory. In contrast, seed harvesting (granivorous) ants destroy the whole diaspore (Berg 1975; Majer & Lamont 1985; Andersen 1990; Majer 1990; Hughes & Westoby 1992a).

Myrmecochory is particularly common in the dry sclerophyll vegetation of Australia (Berg 1975; Davidson & Morton 1981a,b; Rice & Westoby 1981) and South Africa (Milewski & Bond 1982). Plants are assumed to benefit from seed dispersal by ants since seeds may be carried to more advantageous germination sites (Handel 1976; Davidson & Morton 1981a,b; but see Drake 1981; Hughes & Westoby 1992a). Seeds that have been handled by ants may also germinate better (Horvitz 1981). Furthermore, seed dispersal by ants may allow colonisation of more distant habitats, and dispersed seedlings may escape competition from parent plants and siblings (Berg 1975). Finally, seeds inside the ant nest may be protected from fire (Berg 1975) and predators (Heithaus 1981). The ants, in return, benefit from their myrmecochorous behaviour since the elaiosome is rich in lipids and vitamins (Bresinsky 1963; Beattie 1985; Oostermeijer 1989; Hughes & Westoby 1992b).

Viable seeds of *Hibbertia* (Dilleniaceae) are partly or completely enclosed by a pulpy aril. Ants are important dispersal agents of seeds of *H. vestitata*, *H. obtusifolia* and *H. ovata* (Drake

1981; Berg 1975; Hughes & Westoby 1992b) in Eastern Australia, and it has been shown for *Hibbertia ovata* that the aril functions as an elaiosome (Hughes & Westoby 1992b). The only observations on seed dispersal for Western Australian *Hibbertia* species are for *H. cuneiformis*. Seeds of this species are enclosed by a pulpy, bright orange aril and are collected by birds (N Marchant, quoted in Stebbins & Hoogland 1976).

Hibbertia hypericoides, the "Yellow Buttercup" is widespread in low banksia woodlands from Augusta to Northampton, Western Australia (Wheeler 1987), and often dominates the understorey of a site. Mature seeds are either brown, red or black. Brown and red seeds have a short transparent aril, but black seeds are almost fully enclosed by a white, pulpy aril. Black seeds contain firm, white endosperm, but brown and red seeds are characterized by shrivelled or no endosperm. Hence only black seeds are potentially viable. Initial observations indicate that ants collect the seeds of *H. hypericoides* soon after they have dropped to the ground.

Here we describe seed collecting ants and the amount and type of seeds taken, and examine the following hypotheses: (1) ants collect potentially viable seeds more often than non-viable seeds, (2) the aril is rich in lipids, (3) ants are attracted to the aril, and (4) germination of seeds as well as survival and growth of seedlings is higher in ant nests than elsewhere in the same habitat.

METHODS

Study sites and voucher deposition

Field study sites were in Kings Park and Wireless Hill Park, both within the Perth metropolitan area, Western Australia (115°50' E, 31°56' S), and Cooljarloo, ca. 200 km north of Perth near Cataby (115°35' E, 32°0' S). The natural bushland of Kings Park and Wireless Hill Park is character-

ized by low banksia-sheoak woodland (*Banksia attenuata*, *B. menziesii*, *Allocasuarina fraseriana*, *A. humilis*) with jarrah (*Eucalyptus marginata*) and marri (*E. calophylla*) interspersed. *Hibbertia hypericoides* dominates the understorey, with individual plants on average between 3 and 5 m apart. Other common understorey plants are *Macrozamia riedlei*, *Xanthorrhoea preissii*, *Stirlingia latifolia*, *Hypocalymma robustum* and *Jacksonia sternbergiana*. The natural bushland at Cataby is open low banksia-sheoak woodland interspersed with various *Melaleuca* species, *Conospermum stoechadis* and *Hypocalymma robustum*.

Plants with ripe fruits were visited in Kings Park, Wireless Hill Park and at Cooljarloo in December 1990. Seed collecting ants were recorded and sampled for subsequent identification. Voucher specimens are held in a reference collection at the School of Biology, Curtin University or in the Australian National Insect Collection. When species names were unavailable they are either identified with Curtin University code numbers (JDM) or, if voucher specimens are deposited there, with Australian National Insect Collection codes (ANIC).

Seed yield

During December 1990 a total of 40 nests of the most significant seed collecting ant species were visited in Kings Park and Wireless Hill Park. At Cooljarloo 16 nests were visited. The numbers and types of *H. hypericoides* seeds in the refuse heaps were counted, then the upper 30 cm of the soil layer of each nest was removed in order to determine the number and type of seeds inside the nest (Shea *et al.* 1979 found no seeds buried deeper than 30 cm by ants of *Melophorus* sp. 1 (ANIC) in the southern jarrah forest). The distance between each ant nest and the nearest *H. hypericoides* plant was recorded.

Lipid content of seed and aril

Since the nutritional value of seed and aril is mainly due to lipids, a chemical analysis was carried out in order determine the lipid content of seed and aril in *H. hypericoides*. Diaspores (black seeds with pulpy aril) were collected in December 1990 in the Perth metropolitan area, and the aril was removed. Seventy five mg of both arils and seeds were analysed for lipids.

Samples were homogenised with 2 ml of isopropanol; 3 ml of hexane was then added to each sample, and the mixtures allowed to stand for 12 h at room temperature. The supernatants were removed and the residues re-extracted using the same procedure. Supernatants were pooled for each sample and evaporated either under vacuum or with nitrogen. The residues, which contained the "lipid fraction", were weighed to establish the yield.

Lipid fractions (10-50 mg) dissolved in toluene were subjected to a methylation process by adding 4 ml of 1% sulphuric acid in methanol and allowing to stand for 12 h at 50°C. Five ml of 5% aqueous sodium chloride solution was added to each sample, followed by 5 ml of hexane. The mixtures were thoroughly shaken and allowed to separate. The supernatant from each mixture was removed and the residue re-extracted with an additional 5 ml of hexane. Supernatants for each sample were pooled and then passed through a column of anhydrous sodium sulphate. These

methyated lipid fractions in hexane were used for gas-chromatograph/mass-spectrograph analyses.

The methyated lipid fractions, which contained methyated fatty acids (FAMES) were analysed using an Hewlett Packard GC-MS (Model 5971). Chromatography was performed with an Econocap[®] Carbowax 20M column (ID 0.32 mm and film thickness 0.25 μ) using helium as the carrier gas. The initial column temperature was 50°C for 5 min, followed by an increasing gradient of 5°C min⁻¹ to a temperature of 240°C, with the latter temperature being held for at least another 20 min. Run times were approximately one hour. FAMES were identified by using known retention times of standards, and mass spectra.

Attractiveness of the aril

A choice experiment was conducted to determine if the aril is the main attractant to ants of *Melophorus* sp.1. Fifteen of their nests were randomly selected in Kings Park in December 1990. Three seeds, one black and shiny seed with a pulpy aril, one brown seed with a short, brittle aril, and one black seed without an aril (the aril had been removed with forceps), were placed 50 cm away from each nest. Ant behaviour towards these seeds was observed in terms of the time ants spent attending the seeds, whether the aril was consumed and whether the seeds were carried into the nest. All observations were made from 10 am to 1 pm, when temperatures were above 25°C.

Effect of soil on germination

The following experiment was performed in order to test whether the soil inside ant nests is beneficial to the germination of *H. hypericoides* seeds. Freshly collected (in 1990) black seeds were air dried for 3 weeks at room temperature and then planted in sand trays. Sand was collected from the natural habitat in Kings Park. Sand was taken randomly (from any open area which was not close to an ant nest), from underneath *H. hypericoides* bushes, and from ant nests of *Melophorus* sp. JDM 358. Sterilized coarse river sand was used as a fourth treatment. Between 3 and 6 sand trays were prepared with each of the four soil types, twenty five seeds placed in each. All trays were prepared at the end of December 1990 and left unwatered in the glass house of the School of Environmental Biology until the 20th of March 1991, when watering commenced. Surface soil temperatures from December to February ranged from 30 to 45°C during the day. The number of germinating seeds was counted every second day until the 30th of September 1991, when watering ceased. Watering of the trays re-commenced in March 1992, and the number of germinating seeds was counted regularly until the beginning of September 1992.

Survival of seedlings in the field

In Kings Park and Wireless Hill Park, plants and ant nests were scrutinised for seedlings in December 1991. Seedlings were tagged with flagging tape, re-visited in June 1992, and the number of surviving seedlings was recorded.

RESULTS

Ants as seed collectors

Ant species observed collecting seeds of *H. hypericoides* in the study sites belong to the genera *Melophorus* (Family Formicinae), *Rhytidoponera* (Fam. Ponerinae) and *Iridomyrmex*

(Fam. Dolichoderinae). *Melophorus* sp. JDM 358 was the main collector of *H. hypericoides* seed in Kings Park and Wireless Hill Park in 1990 (Table 1). Other ants taking seeds of *H. hypericoides* are *Melophorus* sp. 1 (ANIC), *Iridomyrmex discors* (Forel) and *Rhytidoponera violacea* (Forel). At Cooljarloo, *Rhytidoponera violacea* (Forel) and a species of the *Iridomyrmex rufoniger* group removed seeds of *H. hypericoides* (Table 1).

Attractiveness of the aril

The aril of potentially viable seeds of *H. hypericoides* functions as an elaiosome. *Melophorus* sp. JDM 358 is attracted to the aril of potentially viable seeds. Ants either take black seeds which are enclosed by an aril to the nest immediately or consume the aril first and then take the seeds back to the nest. Seeds without arils attached are less frequently

Table 1

Frequency with which different ant species collected seed of *H. hypericoides* as a percentage of the total number of observations (N) in three study sites in December 1990. Dashes: species was not observed in study site.

Site	N	<i>Melophorus</i> sp. JDM 358	<i>Melophorus</i> sp. 1 (ANIC)	<i>R. violacea</i>	<i>I. discors</i>	<i>I. rufoniger</i> group
Kings Park	63	70	20	5	5	—
Wireless Hill	32	100	—	—	—	—
Cooljarloo	16	—	—	70	—	30

Nests of *Melophorus* sp. JDM 358 are abundant in Kings Park and Wireless Hill Park and are on average 1.24 m (n = 24) and 1.5 m (n = 36) respectively from the nearest *Hibbertia* plant. At Cooljarloo, nests of *Rhytidoponera violacea* are on average 1.2 m from the nearest *H. hypericoides* plant (n = 16). In the Perth metropolitan area, *Melophorus* sp.1 (ANIC) and *Melophorus* sp. JDM 358 start building (or re-open) nests from the previous season in September. They collect large numbers of *Hibbertia* petals which are carried inside the nest and subsequently discarded outside the nest on refuse heaps or middens, hours or days later. Ants begin to collect seeds at the end of October and continue until December when the last seeds mature.

Seed yield

Seed numbers were determined in nests of *Melophorus* sp.1 (ANIC) and *Melophorus* sp. JDM 358 at Kings Park, in nests of an unidentified species of the *Iridomyrmex rufiger* group and in nests of *Rhytidoponera violacea* (Forel) at Cooljarloo, as well as in nests of *Melophorus* sp. JDM 358 at Wireless Hill Park. Ants mainly collected potentially viable seeds. Large numbers of black, potentially viable seeds lay discarded in colony middens at all study sites. The numbers of black seeds found around and inside ant nests ranged from 4 (Kings Park) to 49 (Cooljarloo) in 1990. (Kings Park: number of nests = 26, average number of seeds (mean \pm SE) n = 4.3 ± 1.2 ; Wireless Hill Park: 14 nests, n = 9.9 ± 6.9 ; Cooljarloo: 16 nests, n = 48.6 ± 8.4) Of all seeds found, none had the aril still attached. In all three study sites, between 2 and 5% of the seeds were brown. Although plants produce many more brown seeds than black seeds (see Schatral & Fox in press), brown seeds were collected only infrequently.

Lipid content of seed and aril

The most abundant fatty acids, in both seed and aril are oleic acid, linoleic acid, palmitic acid and stearic acid (Table 2). Qualitative differences in the lipid content between seed and aril were not found. One saturated acid, lauric acid (C12:0), the unsaturated fatty acids C16:1(n-7), C16:1 (palmitic acid) and C18:1 (oleic acid) are relatively more abundant in the food body. C18:2 (linoleic acid) is more common in the seed than in the aril.

Table 2

The abundance of fatty acids in seed and aril of *H. hypericoides* (black seeds only). Abundance is expressed as total % and as a ratio to oleic acid.

Fatty acid	Name	SEED		ARIL	
		%	Ratio	%	Ratio
12:0	Lauric	low*	—	0.4	0.8
14:0	Myristic	1.3	3.5	0.7	1.4
16:0	Palmitic	19.8	53.5	26.8	45.9
16:1		2.1	5.8	2	4.3
16:1 (n-7)	Palmitic	0.3	0.9	4.6	9.8
17:0		low*	—	0.31	0.7
18:0	Stearic	8.4	22.7	6.2	13.3
18:1 (n-9)	Oleic	37	100	46.7	100
18:1		0.6	1.7	0	0
18:2 (n-6)	Linoleic	28.4	77	11.0	23.6
18:3 (n-3)	Linolenic	0.6	1.5	0.3	0.7
20:0	Arachioic	0.5	1.5	0.5	1.2

* The amount was too small to be measured accurately.

collected than black seeds with arils. Thus, 80 % of the black seeds with arils were taken back inside nests but only 53.3 and 46.7 % of the brown and black seeds without arils, respectively, were taken. Brown seeds as well as black seeds without arils are attended for significantly shorter time periods (analysis of variance, $F_{2,42} = 5.53$, $p < 0.05$) than seeds with arils (time attended: n = 15; black seeds with aril, 40.4 ± 5.8 min; black seeds without aril, 13.9 ± 2.6 ; brown seeds, 15 ± 2.5 min). After the seeds had been introduced, ants took only a few minutes to detect them. Seeds were usually attended by 2-12 minor morphs simultaneously (ants of the genus *Melophorus* show continuous polymorphism, J Majer, pers. comm.). However, in most cases a major morph helped to carry the seeds inside the nest. The time that elapsed until the ants carried the seeds back to the nest was not significantly different (analysis of variance, $F_{2,21} = 0.014$, NS) for black seeds enclosed by an aril and brown and black seeds without arils respectively (time taken to carry seed to nest: black seeds with aril, n = 11, 34.1 ± 6.3 min; black seeds

without aril, $n = 7$, 34.7 ± 6.5 min; brown seeds, $n = 6$, 35.7 ± 5.7 min).

Ant dispersal and its effect on seed germination

Seed germination is similar in sand collected around ant nests and sand collected elsewhere in the same habitat. During the first season, seeds germinated significantly slower (analysis of variance, $F_{3,15} = 4.28$, $p < 0.05$) in sterile river sand than in any of the three natural soil treatments (Table 3). However, the number of germinating seeds was not different between soil treatments after half of the experimental time period had elapsed and at the end of the experiment (analysis of variance on arcsine transformed data, after 50 % of time; $F_{3,15} = 1.1$, NS; at the end of the experiment; $F_{3,15} = 0.11$, NS). During the second season, seeds started to germinate significantly later in river sand than in any of the natural soil treatments ($F_{3,11} = 14.4$, $p < 0.05$). After half of the experimental time had elapsed, none of the seeds had germinated in river sand but a small percentage of the seeds in the natural soil treatments had done so (Table 3). The number of germinating seeds was not significantly different between the natural soil treatments ($F_{3,8} = 17.11$, $p < 0.05$). At the end of the experiment, the final germination percentage was similar for river sand and the three natural soil treatments ($F_{3,8} = 0.009$, NS).

Table 3

Germination of seeds of *H. hypericoides* (mean \pm SE, %) from 4 soils over two seasons: First day of germination (mean \pm SE), germination (mean \pm SE, %) after half of the experimental time period had elapsed and at the end of the experiment. n = number of replicates (= sand trays, 25 seeds per tray). During the second season, fewer replicates were available since no germination was recorded for several trays.

First Season 1991		First day of Germination	Germination %	
Soil Type	n		After half of the experiment	At the end of experiment
random	5	59 \pm 6.2	10.0 \pm 4.0	11.2 \pm 4.3
bushes	3	76 \pm 8.5	5.3 \pm 2.7	9.3 \pm 5.8
ant nests	5	54 \pm 9.3	6.0 \pm 2.0	6.4 \pm 4.9
river sand	6	108 \pm 15.0	4.3 \pm 4.3	9.3 \pm 4.9

Second Season 1992		First day of Germination	Germination %	
Soil Type	n		After half of the experiment	At the end of experiment
random	4	76 \pm 4.8	4.5 \pm 1.5	5.5 \pm 1.5
bushes	3	65 \pm 2.9	4.5 \pm 0.9	5.0 \pm 0.6
ant nests	4	74 \pm 4.1	3.0 \pm 0.6	4.5 \pm 0.9
river sand	4	123 \pm 10.6	0	6.0 \pm 2.3

Survival of seedlings in the field

Seedlings were found close to, or on, seven of 40 (17.5 %) ant nests at Wireless Hill Park and Kings Park in December 1991. The number of seedlings ranged from 2 to 15 (mean \pm SE, 5.4 ± 1.67). Seedlings were also observed underneath

parent plants, but the average number of germinating seeds was lower; of 60 plants examined, seedlings were detected underneath 19, with the average number of seedlings of 1.3 ± 0.13 . By June 1992, none of the seedlings had survived, regardless of its germination site.

DISCUSSION

Melophorus sp.1 (ANIC) is one of the most significant seed takers in the northern jarrah forest (Majer 1982). These ants collect elaiosomes although they sometimes consume entire seeds, depending on seed size (Majer 1982). However, the species is omnivorous, with arthropod fragments and seeds found scattered around the nests. Other *Melophorus* species are considered granivores (Davidson & Morton 1981a). Details of the ecology of *Melophorus* sp. JDM 358, the most significant collector of *H. hypericoides* seeds in Kings Park, are unknown. At Cooljarloo, *Rhytidoponera violacea* and *Iridomyrmex rufoniger* sp. collect seeds of *H. hypericoides*. In contrast, species of the genus *Iridomyrmex* have never been recorded eating seeds.

Seeds of *H. hypericoides* drop passively to the ground as soon as they are ripe (dispersal mechanism is of the *Viola odorata* type; Sernander 1906; Berg 1975; Drake 1981). Once dropped from the plant onto the ground, the seeds are removed rapidly. Similarly, ants in the dry sclerophyll forest on North Stradbroke Island in Queensland remove virtually all elaiosome bearing seeds within two days of seed fall (Drake 1981). The high removal rate of *H. hypericoides* seeds suggests that only few seeds remain underneath the parent plant, and therefore most seedlings would escape competition with the parent plant and possible predators underneath the plant. However, the accumulation of seeds around ant nests may cause strong competition with siblings (see below). It is not known whether seeds of *H. hypericoides*, once collected by elaiosome-consuming ants, are subsequently removed by seed-feeding animals (see Hughes & Westoby 1992b for a discussion of this problem).

Since *Melophorus* sp. JDM 358 removes black seeds of *H. hypericoides* still enclosed by an elaiosome in preference to brown seeds and black seeds without the elaiosome, they must be able to discriminate between these seed types. Ants appear to choose between different seeds on the basis of size and/or the chemical composition of the elaiosome. It has been found that the presence of elaiosomes increases the removal rates by *Rhytidoponera metallica* (Hughes & Westoby 1992b) and other ants (Majer 1982; Oostermeijer 1989; Drake 1981; Hughes & Westoby 1992b). Moreover, ants can distinguish fertile *Eucalyptus regnans* seeds from chaff, and a reducing, sugary substance is regarded as the attractant (Ashton 1979).

The chemical analysis demonstrates that both the aril and seed of *H. hypericoides* are rich in the same fatty acids. The elaiosomes of many plants are rich in lipids, but the composition of the lipids varies between species. Oleic acid is the major fatty acid present in the elaiosomes of *Hepatica americana*, *Viola odorata* and four other ant-dispersed North American herbaceous plants (Marshall *et al.* 1979, Skidmore & Heithaus 1988; Kusmenoglu *et al.* 1989). Oleic acid is also abundant in both elaiosome and seed of *H. hypericoides*. Oleic acid and especially 1,2 diolein, a diglyceride which is derived from oleic acid, are the main attractants for seed

collecting ants (Marshall *et al.* 1979; Skidmore & Heithaus 1988; Brew *et al.* 1989; Kusmenoglu *et al.* 1989; Hughes & Westoby 1992b). In contrast, Bresinsky (1963) suggested that the diglyceride ricinolic acid attracts ants to the elaiosomes of *Viola odorata*. Further studies are necessary to determine which chemical substance in the elaiosome of *H. hypericoides* induces seed carrying behaviour in ants.

Germination of *H. hypericoides* seeds in sand collected from ant nests is not enhanced compared with germination attained from sand collected underneath bushes, randomly collected sand and river sand. However, the conditions inside an ant nest will be more complex than the experimental conditions. Moisture, temperature, aeration and the presence of microorganisms may affect the germination of seeds in nature. Since seeds germinated more slowly in sterile river sand than in the natural soil treatments, river sand may lack nutrients and/or certain micro-organisms that promote the successful germination of seeds in natural soil.

The death rate of seedlings observed in the field may be increased as a result of competition on the ant mounds (Beattie & Lyons 1975; Shea *et al.* 1979), although this hypothesis does not explain the equally high death rate for seedlings that grow underneath parent plants. Competition between siblings would be mainly for nutrients and water. The nutrient content of the soil has not been analysed during the present study on *H. hypericoides*. Majer (1982) has found no differences in total nitrogen or available phosphorus contents between soils from *Melophorus* sp. 1 (ANIC) nests and soils from control areas 1 m away from each nest. In contrast, nutrients are concentrated locally on the mounds of some other ants (Davidson & Morton 1981b). Drake (1981) is sceptical of the hypothesis that ant nests are beneficial germination sites. It is not only that seed dumps may cause high competition between seedlings, but the nests of some myrmecochorous ant species do not appear to offer suitable germination conditions. Nests of *R. metallica*, for instance, are sometimes located in tree trunks and germination is highly unlikely because of the restricted depth of soil available.

Whether the removal of the aril benefits seed germination is unknown for *H. hypericoides* but it promotes germination in *H. cuneiformis* (unpublished data). Similarly, Horvitz (1981) found that the germination of the tropical perennial herb *Calathea microcephala* was enhanced by the removal of the elaiosome.

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